Running head: multiple perturbations on rocky shores

COMPOUNDED PERTURBATIONS IN COASTAL AREAS: CONTRASTING RESPONSES TO NUTRIENT ENRICHMENT AND THE REGIME OF STORM-RELATED DISTURBANCE DEPEND ON LIFE-HISTORY TRAITS

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Summary

1. Natural systems are exposed to compounded perturbations, whose changes in temporal variance can be as important as those in mean intensity for shaping the structure of assemblages. Specifically, climate-related physical disturbances and nutrient inputs due to natural and/or anthropogenic activities occur concomitantly, but experimental tests of the simultaneous effects of changes in the regime of more than one perturbation are generally lacking. Filling this gap is key to understand ecological responses of natural assemblages to climate-related change in the intensity and temporal patterning of physical disturbance combined with other global stressors.

2. Responses to factorial manipulations of nutrient enrichment, mean intensity and temporal variability of storm-like mechanical disturbance were examined, using benthic assemblages of tide-pools as model system.

3. Response variables were mean abundance values and temporal variances of taxa with different life-traits. Consistent negative effects of disturbance intensity were observed for the mean cover of long-living taxa (algal canopies and the polychaete *Sabellaria alveolata*), whose temporal fluctuations were also reduced by more severe mechanical stress. More resilient taxa (ephemeral algae, mostly green of the genus *Ulva*) increased under enriched conditions, particularly when low intensity events were irregularly applied over time. Opposite effects of disturbance intensity depending on nutrient availability occurred on filamentous algae (e.g. red of the genus *Ceramium*). This was probably due to the fact that, although nutrient enrichment stimulated the abundance of both algal groups, when this condition was combined with relatively mild physical disturbance the competitively superior ephemeral green algae tended to become dominant over filamentous red algae. The same did not occur under high intensity of disturbance since it likely damaged large, foliose fronds of *Ulva*-like forms more than small, filamentous fronds of *Ceramium*-like forms. Grazers were positively affected by nutrients, likely responding indirectly to more food available.

4. A direct relationship between the mean abundance of most organisms and their temporal fluctuations was documented. However, all organisms persisted throughout the study, even under experimental conditions associated to the largest temporal variation of their abundance, likely due to their ability to resist to/quickly recover from, the applied perturbations. Therefore, in systems with great recovery abilities of dominant organisms (e.g. rocky intertidal, grasslands), effects of traits of the regime of disturbance and nutrient enrichment may modulate the fluctuations of populations not through the elimination and substitution of species, but through changes in relative abundances of the same species. This contrasts with the theory that temporal variation in abundance would be directly related to the risk of local extinction. Present findings enable more accurate predictions of the consequences of climatic and non-climatic scenarios on the biodiversity of marine and terrestrial systems sharing analogous functional traits of organisms. Future more intense physical disturbances are expected to exert negative effects on slow growing/recovering species (e.g. habitat-formers) irrespectively of the temporal patterning of the same disturbances and nutrient inputs. On the contrary, more resistant species (e.g. encrusting algae on rocky shores or below-ground vegetation in grasslands) are expected to benefit from intense physical disturbance. Species whose abundance is more directly related to the availability of nutrients (e.g. filamentous and ephemeral algae or herbs) are expected to generally increase under enriched conditions, but their ability to eventually become dominant would depend on their ability to grow fast and attain cover large enough to overwhelm any possible control of concomitant disturbance intensity on their abundance. If, such as in the present examined system, virtually all organisms can persist, over the temporal scale of the experiment, under any combination of physical disturbance and nutrient availability, the resulting overall diversity is not predicted to change drastically. Nevertheless, low intensity events evenly distributed and high intensity events irregularly distributed appear as the conditions supporting the highest richness of taxa, independently of the availability of nutrients.

Key-words: climate change, eutrophication, mean intensity, rocky intertidal, storminess, temporal variance

Introduction

Human disturbances are critical drivers of changes on spatial and temporal patterns of distribution, abundance and diversity of populations and assemblages in both terrestrial (Ellis *et al.* 2010; Tognetti & Chaneton 2015) and marine (Halpern *et al.* 2008; Doney *et al.* 2012) systems. Anthropogenic transformations of the environment, occurring at faster rates than most natural disturbances, threaten the ability of natural systems to maintain their basic processes, making the understanding of the consequences of such changes a main focus of ecology (Thomas *et al.* 2004; Ruokolainen *et al.* 2009) and society (Lubchenco 1998; Costanza *et al.* 2014).

A key challenge in the study of disturbance is its variability in a range of attributes, including the intensity, timing and extent of individual events (Sousa 1984; Pickett & White 1985) and the temporal and spatial patterns changing in frequency (Collins 2000; McCabe & Gotelli 2000), variance (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; Pausas, Lloret & Vilá 2006; Buckley & Kingsolver 2011; García-Molinos & Donohue 2010, 2011) and correlation (Banitz *et al.* 2008; Tamburello *et al.* 2014). Despite this complexity, a number of past studies have focused on a single trait of disturbance, such as its mean intensity or spatial extent as drivers of biological invasions (Belote *et al.* 2008; Clark & Johnston 2011), or have assumed steady levels of stress along gradients through time, such as experimental tests of the influence of increasingly harsher environmental conditions on negative vs. positive biological interactions (Brooker *et al.* 2008). Following the recognition of confounding issues inherent in the traditional approach of manipulating temporal variability in terms of frequency of events and the implementation of a framework suitable to separate the effects of variability *per se* from those of the overall intensity of disturbance (Benedetti-Cecchi 2003), several studies have involved crossed levels of intensity and temporal variance of disturbance. Manipulative (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; García-Molinos & Donohue 2010; Miller, Roxburgh & Shea 2011) and simulation (Bulleri *et al.* 2014) studies provided evidence that changes in the temporal variance of disturbance can be as important as those of the mean intensity for shaping the structure of exposed assemblages. Such findings are crucial to understand and predict responses of populations and assemblages under climate change characterized by alterations of the mean intensity and temporal variability of meteorological variables (Easterling *et al.* 2000, Maestre, Salguero-Gómez & Quero 2012).

In addition, natural systems are exposed to compounded perturbations interacting with each other in complex ways (Paine, Tegner & Johnson 1998; Clark & Johnston 2005; Martone & Wasson 2008; Pincebourde *et al.* 2012). Climate-related events, in particular, occur in complex combinations (Darling & Côté 2008), but have been examined simultaneously only in relatively few cases (e.g. Martin & Gattuso 2009; Russell *et al.* 2009; Connell & Russell 2010).

Multiple anthropogenic stressors may alter the structure of communities by causing the elimination/decline of some species and the appearance/increase in abundance of others able to take advantage of new resources made available (Grime 1998; Zavaleta *et al.* 2009). Examining how and under which circumstances such shifts occur is needed in both terrestrial and marine habitats. Specifically, human-dominated landscapes are increasingly reduced to patches of native vegetation embedded in larger areas converted to agriculture and pasture (Ellis *et al.* 2010). Human disturbances, such as burning for ultimate agriculture purposes and grazing by cattle (e.g. Laterra *et al.* 2003; Westerling *et al.* 2006), can directly affect dominant plant species (Mazía *et al.* 2010) and indirectly modify the availability of resources, including soil nutrients (Gross, Mittelbach & Reynolds 2005; Besaw *et al.* 2011). Analogously, marine coastal systems are exposed to the impact of waves during storms and to increases of nutrient inputs due to terrestrial runoff associated with the overuse of land and deforestation (Ambasht

& Ambasht 2003). Nutrient inputs into coastal systems are a global phenomenon which has increased in the last decades, with direct positive effects on primary producers (Nielsen 2001) and indirect interactions with biological processes, including grazing (Worm, Lotze & Sommer 2000; Hillebrand 2003). Climate change-related physical disturbance and nutrient inputs/availability are strictly interlinked through increasing erosion and runoff due to the anthropogenic alteration of the hydrological cycle (French 1997). In fact, changes in the intensity and in spatial and temporal patterns of precipitation, usually associated with storms, are positively related to the delivery to coastal waters of nutrient-rich water from inland agricultural fields, industrial plants and urban areas (e.g. McClelland & Valiela 1998; Cloern 2001; DeBruyn & Rasmussen 2002).

It is widely recognized that disturbance can critically shape community structure through positive and negative mechanisms critically depending on life-traits of exposed organisms (e.g. Huston 1994). Dominant organisms can be removed proportionally to the intensity of disturbance (e.g. Benedetti-Cecchi 2000), consequently releasing resources usable by other species (Shumway & Bertness 1994; Bertocci *et al.* 2005). As indicated by a number of classical studies, the response of individual taxa to possibly analogous disturbances is driven by their ability to cope with the balance between increased mortality/emigration and the availability of opportunities for colonization/immigration determined by the release of new resources (Connell 1978; Huston 1979, 1984; Sousa 1979, 1984; Pickett & White 1985; Connell, Hughes & Wallace 1997). For example, the timing of disturbance relative to that of reproduction and recruitment of organisms is key to modulate their actual ability to colonize disturbed habitats (Dayton *et al.* 1984; Breitburg 1985), while disturbed patches differing in size and isolation can be re-occupied by species with different dispersal and competitive abilities (Keough 1984; Shumway & Bertness 1994). On the other hand, nutrients can increase algal productivity, especially under reduced grazing pressure, but the abundance of herbivores can be decoupled from that of resources depending on their preferences for more palatable food, such as non-calcified algae in tide pools (Nielsen 2001).

However, several previous experimental and observational studies aimed at examining general responses of populations and assemblages to disturbance have overlooked the effects of productivity (e.g. Mackey & Currie 2001), while taking them into account is required to assess general disturbance/species diversity relationships (Huston 2014). Simultaneous manipulations of multiple traits (mean intensity and temporal variance) of mechanical disturbance and the availability of nutrients are needed to test for their interactions under realistic scenarios of compounded environmental stressors (but see Bertocci *et al.* 2015).

The present study used benthic assemblages of algae and invertebrates from tide-pools as model system to contribute to fill this gap. Assemblages from rocky intertidal habitats were considered a convenient study system as they are exposed to variable physical conditions that can affect their structure or even become detrimental to their life (Bertness & Leonard 1997). Specifically, increasing intensity and temporal variability of storms and precipitation may enhance physical disturbance (Underwood 1998) and nutrient inputs (Díez *et al.* 1999), which,, possibly modulated by biological interactions (Dayton 1971; Levin & Paine 1974; Williams, Bracken & Jones 2013), may exert quantifiable effects on such assemblages.

Levels of intensity and temporal variability, intended as changes in the variance of events with the same overall frequency, of storm-like mechanical disturbance and nutrient enrichment were manipulated in a multi-factorial design, examining mean values and temporal fluctuations of abundance of individual taxa and of the richness of taxa as response variables. It was hypothesized that the combination of large variance and severe intensity of disturbance could determine markedly different responses depending on life-traits of organisms (Fig. 1). In fact, large temporal variance implies that several events occur over short intervals, alternating with prolonged periods lacking disturbance (Benedetti-Cecchi 2003). Therefore, populations of relatively long-living species characterized by episodic recruitment and/or low dispersal (Caley *et al.* 1996), such as habitat-forming macroalgae and invertebrates, would be exposed to more extreme physical conditions under disturbance events occurring with large, compared to small, temporal variance. On the contrary, ephemeral species might take advantage of the same condition as a consequence of the released resources (Dayton 1971). Such effects were expected to be related to the mean intensity of disturbance as it was reasonable to assume that effects characterized by the same temporal variance were exacerbated by higher, compared to lower, intensity. Specifically, a series of intense disturbances operating at short intervals was predicted to reduce the mean value and, thus, to dampen the temporal fluctuations of abundance of less resilient taxa over the experimental period (Taylor 1961). Taxa with quick recovery ability, instead, even if temporarily reduced by intense disturbance, would have re-established large densities in short times, which, combined with the effect of the concomitant reduction of potential competitors, would have determined larger mean values and larger fluctuations in abundance under high intensity and large variance compared to low intensity and small variance of disturbance. Effects of intensity and temporal variability of disturbance, however, were hypothesized to depend on the increased availability of nutrients, which can determine an increase in the abundance of ephemeral, fast-growing macroalgae, often followed by a decline of perennial, slow-growing species (Valiela *et al.* 1997; Raffaelli, Raven & Poole 1998). If this was true for the studied system, increased concentration of nutrients could have maintained temporally consistent larger abundances of fast-growing (e.g. ephemeral algae) and fast-colonizing (e.g. grazing gastropods) and lower abundances of less resilient (e.g. algal canopies and habitat-forming polychaetes) organisms, counteracting any effect of concomitant disturbance events compared to the natural nutrients conditions. Such issues applied also to the richness of taxa (Fig. 2), as the effects of "extreme" combinations of intensity and variability of disturbance could be expected to reverse between low- and high-nutrient conditions (reviewed by Huston 2014). Low growth rates associated with low productivity could support high levels of richness of taxa only under mild disturbances causing low levels of mortality, as very severe disturbances would drive populations to extinction. On the contrary, when growth rates associated with high productivity are high, high levels of richness could be determined by severe disturbance causing high levels of mortality required to prevent competitive exclusion. Although this study focused on a single location and particular aspects of environmental change, it addressed the general issue of how climate-related disturbance, changing in mean intensity and temporal variance and combined with other globally relevant anthropogenic stressors, drives patterns of biodiversity in rocky shores and possibly other systems characterized by analogous functions and life-traits of dominant organisms.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

The study was carried out between February 2012 and September 2013 in the mid-shore (0.5 m to 1 m above Chart Datum) tide-pool habitat located along 1 km of rocky coast in northern Portugal (between 41°42'01''N and 41°42'16''N). This system and hosted benthic assemblages are described in detail elsewhere (Bertocci *et al.* 2012, 2015). Briefly, conspicuous elements of assemblages are canopy-forming macroalgae, including the kelp *Laminaria ochroleuca* Bachelot de la Pylaie and the smaller red *Mastocarpus stellatus* (Stackhouse) Guiry, *Chondrus crispus* Stackhouse and *Gigartina pistillata* (S. G. Gmelin) Stackhouse (Bertocci *et al.* 2010), encrusting Corallinales (mostly *Lithophyllum* spp.), red filamentous (e.g. *Ceramium* spp. and *Polysiphonia* spp.) and ephemeral green algae (*Ulva* spp.). Sessile invertebrates are mostly represented by the reef-forming polychaete *Sabellaria alveolata* (L.), and grazers by top-shells (*Gibbula* spp.), limpets (*Patella* spp.) and sea urchins (*Paracentrotus lividus* Lamarck).

At the beginning of the study, three pools were left unmanipulated as control and three were randomly assigned to each combination of the following treatments: intensity (low vs. high), temporal variability (small vs. large, represented by regular or irregular distribution of events, respectively) and sequence (two temporal patterns, replicated only within the large, irregular level of variability) of mechanical disturbance, and nutrient availability (natural vs. enriched). Three 35 x 35 cm plots were marked in each pool (Fig. 3 A). Experimental disturbance, simulating the mechanical impact of waves during severe storms (Bertocci *et al.* 2005), was performed by battering the substratum of each plot with a rubber-covered chisel mounted on a battery hammer. The area of each plot was disturbed once or twice in a row to produce, respectively, the low (LI) and the high (HI) level of intensity. The temporal variability was manipulated (see Fig. 3 B) by performing a total of five events of disturbance distributed regularly at four-months intervals (small level: Reg) or irregularly (large level: Irr) according to clustered events interspersed within longer periods lacking disturbance (Benedetti-Cecchi 2003; Bertocci *et al.* 2005). Two random sequences (S1 and S2) of events characterized by the same value of variance of the intervals of time between consecutive disturbances were replicated within the Irr level to separate the actual effects of temporal variability from those of the particular pattern of events used to produce the intended level of variability. Nutrient enrichment was produced by deploying 200 g of slow-release fertilizer pellets (Osmocote® Exact® Standard, NPK: 15-3.9-9.1 + 1.5 Mg) in each of two PVC dispensers applied in each pool assigned to this treatment. Pellets were replaced every two months. Full details on experimental procedures and design, data on the effectiveness of the enrichment treatment and information on the links between manipulated and natural events of disturbance are reported in Bertocci *et al.* (2015).

SAMPLING AND STATISTICAL ANALYSES

The percentage cover of sessile organisms and the number of individuals of mobile animals were visually (Dethier *et al.* 1993) estimated, in the three plots of each pool, at each of ten times established over the duration of the experiment, as illustrated in Fig. 3.

The mean value and the temporal variance of the abundance of conspicuous taxa and of the richness of taxa were analysed with ANOVA, for which the three plots in each pool were averaged and the three pools assigned to each experimental condition provided the replicates. The analysis was based on an asymmetrical design involving the partitioning of the total variability into the 'Control vs. Treatments' contrast and the 'Among treatments' variation. The latter was also partitioned into the main effect of each factor and their interactions, with the 'Temporal variability' of disturbance further partitioned into a 'Reg vs. Irr' and a 'Between sequences' contrast. The assumption of homogeneity of variances was assessed with Cochran's test and data were log-transformed if necessary. The details of analyses are reported in Supplementary information (SI 1) and Bertocci *et al.* (2015). When relevant, Student-Newman-Keuls (SNK) tests were used for post-hoc comparisons of means.

Results

A total of 57 taxa (39 macroalgae and 18 invertebrates: see Supplementary information SI 2) were identified over the experiment and provided the examined total richness of taxa or were collapsed, as relevant, into four morpho-functional algal groups (canopy-forming, filamentous, ephemeral green, encrusting) and the grazers. Single taxa showed idiosyncratic responses to the treatments (detailed analyses reported in SI 1).

The mean and the temporal variance in the abundance of habitat-formers, i.e. canopy-forming macroalgae (Fig. 4 A and 5 A) and the polychaete *S. alveolata* (Fig. 4 B and 5 B), were significantly larger in the low than in the high intensity treatment, independently of other experimental conditions.

The intensity of disturbance also affected the mean abundance and the temporal variance of filamentous algae, but in opposite directions depending on the availability of nutrients. Under the natural condition, both response variables attained larger values in the low compared to the high intensity treatment, while this pattern reversed in the enriched condition

(Fig. 4 C and 5 C1). In addition, when disturbance events were applied at regular intervals, the natural condition maintained the temporal variance in abundance of this algal group larger compared to the enriched condition, while the opposite effect of nutrients occurred in the irregular treatment (Fig. 5 C2).

The mean percentage cover of ephemeral green algae was significantly lower in control than, on average, all other pools (Fig. 4 D). In treated pools, however, these algae were affected by the interaction between nutrients, the intensity and the sequence of irregularly distributed disturbance events. Low intensity events applied according to sequence 2 (S2) under the natural condition determined larger mean and larger temporal variance of cover compared to the other combinations of intensities and sequences (Fig. 4 D and 5 D). Under the enriched condition, the mean abundance of ephemeral green algae was larger in the low than in the high intensity treatment independently of the sequence of disturbance (Fig. 3 D), while the temporal variance was larger for low intensity events applied according to sequence 1 (S1) than in all other experimental combinations (Fig. 5 D).

The mean abundance of encrusting corallines was larger in the high than the low intensity treatment independently of all other treatments (Fig. 4 E1) and in the enriched than in the natural condition, but only when disturbance events were established according to S1 (Fig. 4 E2). The temporal variance in the percentage cover of this group was significantly reduced in control than, on average, treated pools. Moreover, this response variable was increased by low, compared to high, intensity events applied according to the regular and the S1 pattern, while the opposite effect of intensity was shown under S2 (Fig. 5 E).

Grazers were consistently more abundant in enriched than in natural pools (Fig. 4 F). Nutrients had a positive effect also on their temporal variance, but only combined with regularly distributed disturbances, as no significant effects of nutrients were found under irregular events (Fig. 5 F).

Regularly distributed disturbances were associated with a larger richness of taxa when applied at low compared to high intensity, while the opposite effect of intensity was observed under irregular events (Fig. 4 G). Low intensity of regularly distributed events also increased, compared to high intensity, the temporal variance of richness, while disturbance intensity did not exert significant effects on this variable when events were applied irregularly (Fig. 5 G). Variations in the abundance of each taxon and in the total richness over the period of the experiment are illustrated in Supplementary information (SI 3).

Discussion

Present findings supported the proposed hypotheses only in terms of some aspects related to the general direction of responses to the manipulated factors, but not in terms of the interactions among them. Specifically, the mean abundance of the most structured species (canopy-forming algae and *S. alveolata*) was inversely related to the intensity of disturbance, but this response was not modulated by the other treatments. It has been demonstrated that even algae well adapted to very exposed areas can be removed by extreme storms due to the wave force itself and to the impact of rolling rocks (Shanks & Wright 1986; Denny *et al.* 1989). These mechanisms are most likely to occur for arborescent species, such as the present canopy-former *C. crispus* and kelps, for which extensive dislodgement has been observed due to winter storms (Seymour *et al.* 1989; Dudgeon & Johnson 1992). In fact, extreme waves can exert self-reinforcing negative effects on algal beds once they open patches within an originally aggregated canopy, thus exposing the remaining individuals to increased hydrodynamic forces (Boller & Carringron 2006). Analogously, *S. alveolata* reefs are extremely sensitive to natural (storms) and human (trampling) mechanical disturbance which can critically damage the adult bio-constructions and reduce the density of recruits (Dubois *et al.* 2006). In general, such mechanisms are classically known to contribute to make wave-generated disturbance a key driver of the structure of intertidal assemblages on rocky shores (Dayton 1971) and may also explain the overwhelming effect, not initially hypothesized, of intensity of disturbance compared to those of temporal variability and nutrient enrichment on slow-growing habitat-formers. Moreover, this effect was likely exacerbated by the slower recovery ability of such organisms compared to potential competitors. It was documented, in particular, that limited damage of *S. alveolata* reefs can be repaired in some weeks through the tube-building activity (e.g. Plicanti *et al.* 2016), but the recovery of severely disturbed reefs critically depends on other processes, such as larval supply, occurring at much larger time scales (Ayata *et al.* 2009). Large variations in recruitment of *S. alveolata* were documented over periods up to years (Gruet 1986), a time scale which is clearly larger than the longest time for recovery available to this species to recolonize after disturbance in the present experiment. Analogously, there is evidence that even considerably damaged beds of canopy-forming algae may recover in some months, but large patches where the canopy was completely removed by very intense disturbance take much longer (Underwood 1998; Speidel, Harley & Wohnam 2001). In this context, but in the opposite direction, the main positive response of encrusting coralline algae to disturbance intensity is consistent with their described poor competitive abilities and great resistance to physical stress (Breitburg 1984). In fact, unlike algal canopies, even intense mechanical disturbances are unlikely to completely eliminate these forms, which can then quickly re-grow from the crust. Such traits typically make them dominant in physically and/or biologically harsh habitats where potential competitors are eliminated (Steneck 1986; Bertocci *et al.* 2005; McCoy & Kamenos 2015). According to such interactions, however, the observed increase, though modulated by the sequence of disturbance events, in the abundance of this algal group in enriched pools, where several erect algae were also more abundant, could be puzzling based on the present original hypotheses. The productivity of encrusting corallines, however, can be directly enhanced by nutrient enrichment (Smith, Smith & Hunter 2001), while the ability to tolerate overgrowth for relatively long periods (Underwood 2006) may allow these algae to take advantage of the ameliorated environment provided by the upper algal layer (Figueiredo, Kain & Norton 2000). The dependence of the effect of nutrients on the sequence of disturbances is more difficult to interpret, but likely involved direct and indirect causes. For instance, encrusting corallines can quickly recover in disturbed patches through vegetative growth (Steneck 1986) and field measurements from the same geographic area have indicated no growth of several species during winter (October to March) and maximum growth rates during summer (June-July) (Adey & McKibbin 1970). In summer, present irregular, sequence 1 treatment included more (two versus one) events of disturbance than sequence 2 treatment and this may have implied temporary more stressful conditions for potential competitors, concomitantly to nutrient and life-cycle conditions determining the peak of growth of encrusting corallines.

Increasing availability of nutrients is known to directly stimulate the abundance and growth of ephemeral and epiphytic macroalgae in coastal habitats (Valiela *et al.* 1997; Masterson *et al.* 2008), which is, as in general originally hypothesized, consistent with the general increase in abundance of red filamentous and ephemeral green algae in present enriched pools. More interesting and somehow unexpected were the interactive effects, as the high intensity treatment combined with the natural nutrient condition reduced, compared to the low intensity treatment, the cover of the first group, while the effect of intensity reversed under the enriched condition. These findings can be interpreted by first noting that red filamentous species of the genus *Ceramium* can become nutrient-limited in very oligotrophic waters (Pedersen, Borum & Leck Fotel 2010). Even without reaching such an extreme, this makes logically explainable that the high experimental intensity of disturbance reduced the cover of this algal group when combined with the natural condition, where growth was likely lower than in the enriched treatment. On the contrary, nutrient enrichment could have determined faster growth rates of filamentous algae, consequently buffering the negative effect of severe disturbance. Eventually, this effect might have reversed to positive through the reduction of algal canopies, as generally observed here and invoked as a main mechanism for the replacement of perennial macroalgae by ephemeral forms (e.g. Valiela *et al.* 1997). The same pattern of responses, however, was not shown by ephemeral green algae, whose abundance was generally increased by the low intensity treatment in enriched pools, but only when disturbances were established according to one irregular sequence (S1). As documented here too, ephemeral green algae of the genus *Ulva* can become dominant under enriched conditions (Raffaelli *et al.* 1998), which, in principle, could have prevented any possible control of intensity of disturbance on their abundance (Masterson *et al.* 2008). The fact that this did not happen, adding to the overall high intensity-associated reduction of potential space-occupying competitors, suggests that direct effects of disturbance on these algae might occur even under high productivity. Analogous evidence was previously provided for biological disturbances, such as grazing (e.g. Paine 2002), rather than for physical factors. Under the natural condition, instead, the specific sequence of events became more relevant to modulate the effect of disturbance intensity. The specific mechanisms of such response still need to be elucidated, but they might involve interactions between the timing of experimental disturbance and factors responsible for the natural temporal variation of abundance of ephemeral green algae (see control trajectories in SI 2). For example, competition for space could have contributed to the general inverse response of filamentous red algae and ephemeral green algae to the intensity of disturbance combined with nutrient enrichment. In such a context, laboratory experiments have indicated that, under eutrophic conditions, the maximum growth rate of *Ulva* spp. can be more than double than that of filamentous red algae of the genus *Ceramium* (Pedersen & Borum 1997). Both genera were among the most representative of the filamentous red and the ephemeral green algal group here examined. So, it can be hypothesized that, although both groups increased in abundance due to nutrient enrichment, competitively superior ephemeral green algae tended to become dominant over filamentous red algae, but that this outcome could be, at least in part, buffered by high intensity of physical disturbance which was likely to damage the large, foliose fronds of *Ulva*-like forms more than the small, filamentous fronds of

Ceramium-like forms. The lack of clear inverse patterns of abundance of the two algal groups during the course of the experiment did not provide full support to this mechanism, but it is worth noting that the largest peaks of cover of filamentous red algae were measured at the last time of sampling, concomitantly with some of the smallest recorded cover values of ephemeral green algae. Moreover, the overall consistent patterns of abundance of palatable algae, such as filamentous and ephemeral species, and grazers in response to nutrients suggest that increases/decreases in the availability of food could support analogous variations in the number of herbivores without implying a strong feedback-control by grazing even where grazers were more abundant. The stimulation of macroalgal blooms by enhanced nutrient supply, in spite of the top-down control by herbivores, has been documented in other tide-pool systems (Masterson *et al.* 2008).

In terms of overall diversity, regularly and irregularly distributed events determined a switch from a negative to a positive effect of high intensity of disturbance on the richness of taxa. It seems, therefore, that low intensity events evenly distributed and high intensity events irregularly distributed were the conditions able to support the highest richness of taxa over the time scale of the experiment, irrespectively of the availability of nutrients. The independence of effects of intensity and variance of disturbance from nutrient availability led to reject, in general, the proposed hypotheses regarding richness. The hypothesized direct or indirect relationship between disturbance severity and species richness under, respectively natural nutrients or enriched conditions was clearly not supported by present data. Discussing in detail the possible mechanisms for this unexpected outcome is beyond the scope of this study, as they likely involved complex interactions that could not be unequivocally tested by the present experiment. In fact, a recent review regarding general theories on links between traits of disturbance, productivity and species diversity has explicitly illustrated a number of logic and logistic difficulties in unambiguously testing for the effects of all factors and processes responsible for patterns of coexistence or competitive exclusion of species over proper spatial and temporal scales (Huston 2014). For example, it was traditionally postulated that mechanisms responsible for species coexistence, hence for high species diversity, are effective only where competitive exclusion is prevented either by mortality-driven disturbance (Connell 1978; Huston 1979), or by low productivity eventually reducing growth rates, and/or by the combination of both (Huston 1979). Anyway, long-term coexistence of species is unlikely to occur in systems exposed to periodic disturbances and where most species have similar resource requirements (e.g. Huston 2014). It is interesting, however, that a negative effect of high intensity, buffered by high temporal variance, of disturbance (aerial exposure) on the richness of benthic assemblages was reported in another rocky intertidal system (Benedetti-Cecchi *et al.* 2006) as a consequence of the replacement of less diversified (encrusting coralline algae) by more heterogeneous (filamentous algae) groups under such conditions. Given the present results, the same mechanism was unlikely here, while it can be hypothesized that the combination of intensity and temporal variability of disturbance exerted significant effects on the total richness by affecting several taxa that were numerically very rare in the collected samples and not included, for their characteristics, in the groups analyzed individually.

In a broader context, it is worth noting that, in spite of recent advances (e.g. Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; García-Molinos & Donohue 2011; Bulleri *et al.* 2014), current knowledge on ecological effects of environmental change is still based on studies focusing on constant mean levels of relevant variables (Cardinale *et al.* 2002; Hutchings, John & Wijesinghe 2003) or on changes in the mean intensity (Mackey & Currie 2001) or the frequency (Collins 2000; McCabe & Gotelli 2000) of disturbance. Present findings, instead, suggest that examining the circumstances, the scales and in which direction the temporal variance and the mean of disturbance interact is relevant to increase the accuracy of the understanding and predictions of the influences of anthropogenic changes on natural diversity. This is of great importance since changes in disturbance regimes are already apparent and are expected to continue in the future. For example, the temporal patterning and severity of fires in the USA are changing in association with climate warming (Westerling *et al.* 2006); insect outbreaks in forests are occurring over greater extents and involving new sets of species (Raffa *et al.* 2008); data showing trends towards the aggregation of extreme storms in short periods separated by prolonged periods of calm are available for tropical areas (Muller & Stone 2001; Wolff *et al.*. 2016); further increases of both the mean intensity and the temporal variance of meteorological events are predicted by climate models (Michener *et al.* 1997; Easterling *et al.* 2000; Trapp *et al.* 2007); changes in the temporal variance of environmental stress are expected to be as important as those in the mean intensity to modulate shifts between competitive and facilitative interactions (Bulleri *et al.* 2014).

In most cases, differences in temporal variance of abundances tracked those in the mean, with relatively smaller fluctuations occurring in treatments where organisms were, on average, less abundant over the experimental period. This is, in general, interpretable as a consequence of the scaling relationship between the mean and the variance, according to which persistent low mean abundance values would not allow large fluctuations (variances) around them (Taylor 1961). But what might be the ecological consequences of that? There is evidence that temporal variation in abundance may be directly related to the risk of local extinction of species (Lande 1993; Vucetich *et al.* 2000; Inchausti & Halley 2003). Analogously to a previous experiment in a Mediterranean rocky system (Bertocci *et al.* 2005), the analysed organisms did not support this hypothesis as, in spite of temporary even drastic drops in their abundances, all persisted throughout the experiment, likely due to their overall ability to resist to, or quickly recover from, the applied perturbations. It could be predicted that in systems with analogous recovery abilities of dominant organisms, the separated or interactive effects of traits of the regime of disturbance and nutrient enrichment could affect temporal fluctuations of exposed populations not through the elimination and substitution of species, but through changes in relative abundances.

The last point is linked to the question of whether present findings may be generalized to other systems, such as grasslands (Hooper *et al.* 2005), which share high resilience to disturbance and similar "response traits" of organisms with rocky intertidal ones. In fact, disturbances, such as grazing and fires, normally affect the aboveground vegetation, while the belowground vegetation can recover quickly (McNaughton 1985; Cooper, Huffaker & LoFaro 1999; Laterra *et al.* 2003). Moreover, mowing and fire can suppress dominant tussock grasses and facilitate, particularly under increased nutrients, short-lived forbs (Mazía *et al.* 2010; Tognetti & Chaneton 2015). Based on present findings, preponderant effects of physical disturbance intensity, determining a reduction in both the mean abundance and temporal fluctuations of long-living plants, can be hypothesized in grasslands. On the contrary, large increases of ephemeral forbs could be predicted under nutrient enrichment, especially when concomitant with relatively mild events of physical disturbance occurring according irregularly over time. The different ability of species characterized by contrasting life-history traits, however, could drastically shape the final outcome of such mechanisms depending on the tension between the direct response to disturbance and nutrients and the indirect modulation of biological interactions, such as competitive and/or consumer-prey relationships. Analogously, in coral reefs, branched species, such as *Acropora* spp. and *Pocillopora* spp., are more likely to be killed by physical disturbance compared to massive species, such as *Platygyra* spp. and *Porites* spp., but they are also characterized by faster growth and consequent higher recovery ability after disturbance (Marshall & Baird 2000; Loya *et al.* 2001; Baird & Marshall 2002; McClanahan *et al.* 2004). Storm-related damage and recovery of coral reefs, however, are highly variable depending on complex interactions between storm characteristics, reef topography and size and biological traits of organisms (reviewed by Harmelin-Vivien 1994). Making predictions, based on present findings, on responses of coral reefs to analogous changes in environmental conditions is probably even more complicated. For instance, nutrient enrichment is widely considered responsible for observed declines of coral reefs (e.g. Fabricius

2005), but their underlying mechanisms are subject to strong and controversial debate (Szmant 2002; Bell *et al.* 2007). In general, it can be hypothesized that, differently than in rocky intertidal habitats and grasslands, nutrients, either as a single stressor or combined with mechanical disturbance, affect corals not directly, but through their effects on phytoplankton and epiphyte loads. These may ultimately modulate the tolerance of corals to physical stress in complex ways (e.g. D'Angelo & Wiedenmann 2014). Overall, however, there is evidence that such complex interactions may result in healthy and diverse coral reefs within ranges of nutrient concentration and other pressures even broader than expected (D'Angelo & Wiedenmann 2014), which is, at least in part, consistent with the persistence of most species over the course of the present experiment in spite of temporarily 'extreme' conditions. Experiments analogous to the present one are needed to test whether responses similar to those of rocky intertidal systems would occur in grassland and coral reef systems. Nevertheless, to our knowledge, this experiment provided the first manipulative test of the effects of changes in the regime (mean intensity and temporal variance) of climate-related disturbance crossed with levels of a concomitant, globally relevant, stressor. As such, it can provide an advancement and more realistic contribution to understand and predict the ecological implications of variations of compounded perturbations occurring at the global scale as a direct and indirect consequence of anthropogenic activities.

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LEGEND TO FIGURES

Fig. 1. Schematic representation of how intensity and variance of mechanical disturbance and nutrient enrichment can affect patterns of abundance and temporal fluctuations of algal species with different life-traits. Under natural nutrient concentration (- NUTRIENTS), mechanical disturbance events characterized by increasing intensity and variance would be particularly detrimental to long-living/low dispersing species, while they could facilitate ephemeral/high dispersing species by releasing resources. During the course of the experiment, the abundance and temporal fluctuations of the first and the second group are expected to be, respectively, reduced and increased compared to conditions of low intensity and low variance of disturbance. Increased nutrient concentration ('+ NUTRIENTS') would primarily support higher abundance of ephemeral/fast-growing algae, possibly followed by a decline of perennial/slow-growing species. As a result, the enriched condition is expected to maintain temporally consistent larger abundances of fast-growing/fast-colonizing and lower abundances of less resilient organisms, buffering the effects of concomitant mechanical disturbance events compared to the natural nutrients condition.

Fig. 2. Conceptual model showing how intensity and variance of physical disturbance and nutrient enrichment can affect species richness. Under low productivity (natural nutrients: dashed line) and consequent low growth rates, large species richness would be supported only under mild (low intensity and low variance) disturbance, since very severe disturbance (high intensity and large variance) would drive most species to local extinction. Under high productivity (enriched: solid line) and consequent high growth rates, large species richness is expected under severe disturbance able to produce relatively high levels of mortality required to prevent competitive exclusion by few species that would otherwise become dominant.

Fig. 3. Experimental design. A) Schematic representation of the entire design, including two levels of nutrients (enriched and natural), two levels of both intensity (low and high) and temporal variability of mechanical disturbance (regular and irregular), two sequences (S1 and

S2) of events within the irregular treatment, three pools allocated to each combination of such manipulations, and three control (unmanipulated) pools. B) Representation of the distribution of mechanical disturbance events (D) over the course of the experiment, for each level of temporal variability. T1 to T10 are the times of sampling, established provided that the average time elapsed since the previous event of disturbance was the same between all levels of temporal variability and sequences of disturbance (Bertocci et al. 2005). The variance of the intervals of time (in months) between successive disturbances is 0 for the regular and 21 for each irregular treatment.

Fig. 4. Mean (+ SE) abundance over the experimental period of individual taxa and richness of taxa, illustrating significant differences among treatments (SI 1, Table 1). C, LI, HI = unmanipulated control (white), low (light grey), high (dark grey) intensity of disturbance, respectively; Reg, Irr = regular, irregular (two sequences: S1 and S2) pattern of disturbance, respectively; N, E = natural (dotted), enriched (dashed) condition, respectively. Relevant significant tests are reported below each panel. Different letters above bars represent treatments differing significantly at $p<0.05$ (SNK tests).

Fig. 5. Univariate measures of temporal variance of abundance (in logarithmic form) of individual taxa and of the richness of taxa calculated over the period of the experiment, illustrating significant differences among treatments (SI 1, Table 2). Symbols and abbreviations as in Fig. 4.

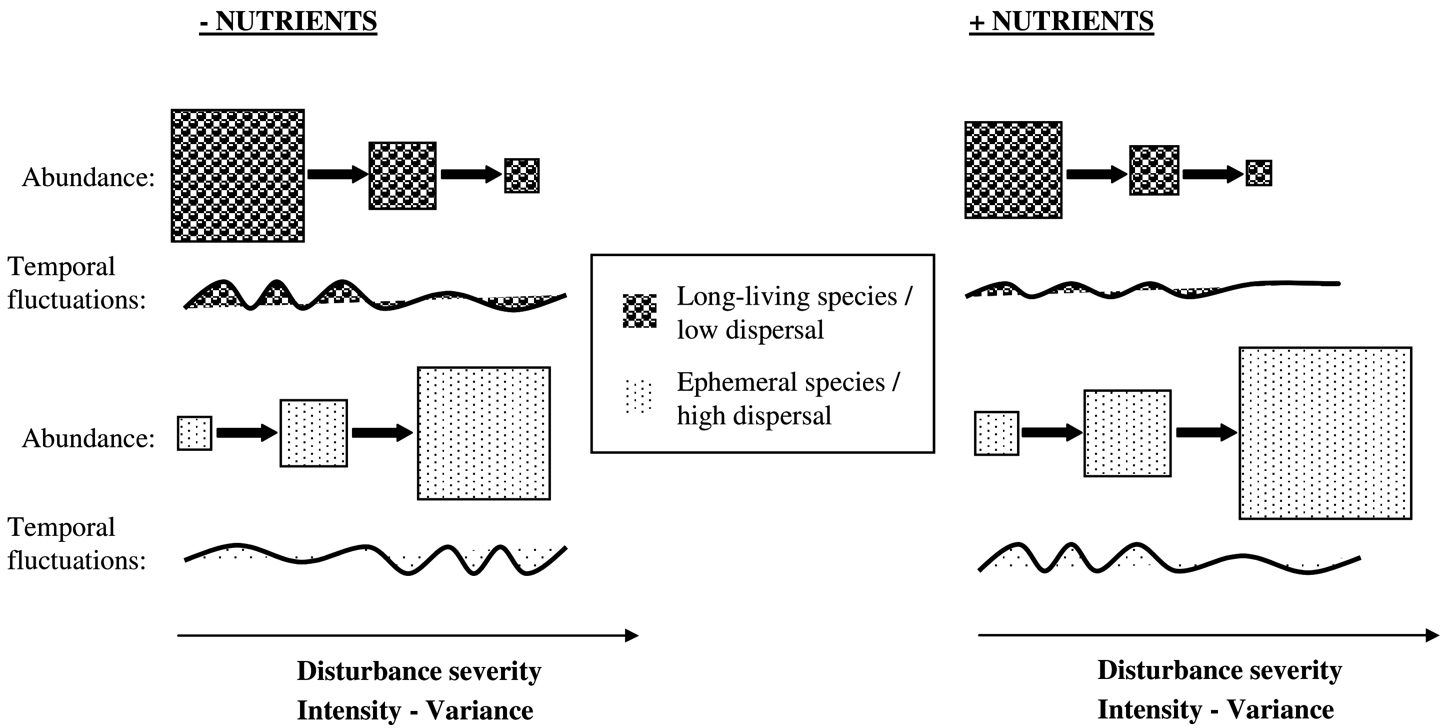


Fig. 1 Bertocci et al.

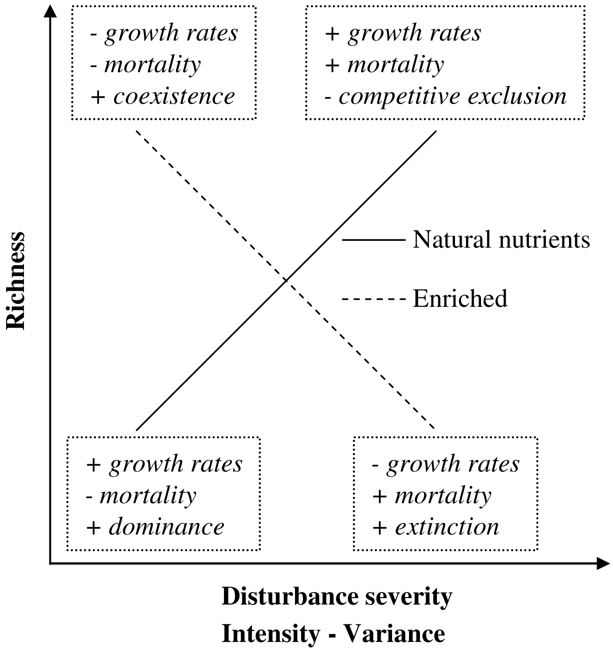
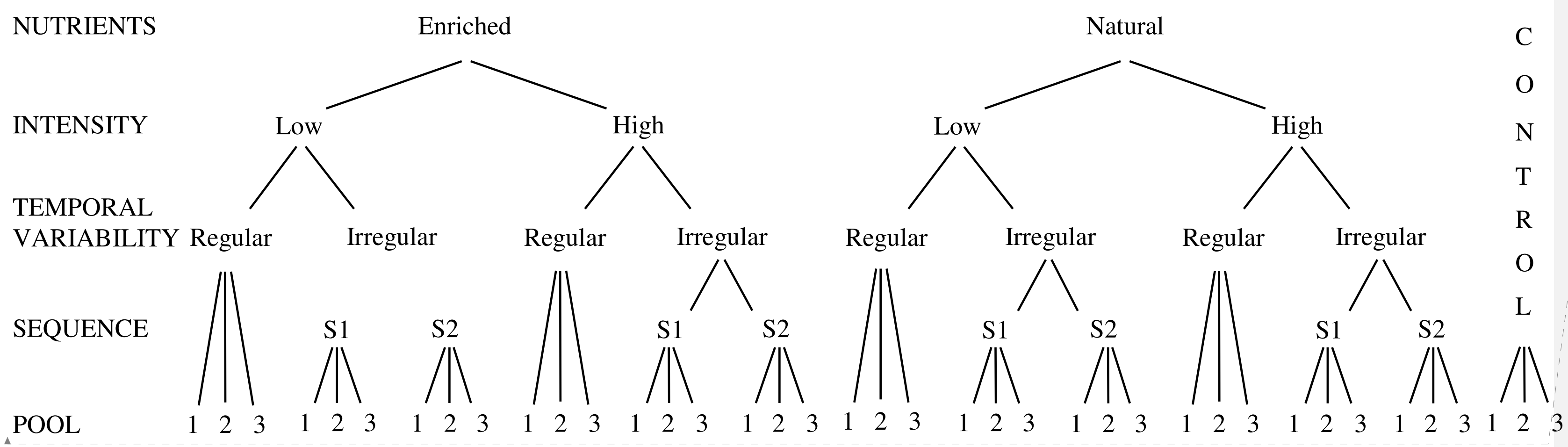


Fig. 2 Bertocci et al.

A)



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B)

REGULAR TREATMENT

	D				**D**				**D**				**D**				**D**		

IRREGULAR TREATMENT (Sequence S1)

		D		**D**						**D**						**D**	**D**		

IRREGULAR TREATMENT (Sequence S2)

		D	**D**		**D**						**D**						**D**		
			T1	T2	T3		T4	T5	T6			T7				T8	T9		T10
Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
2012											2013								

Fig. 3 Bertocci et al.

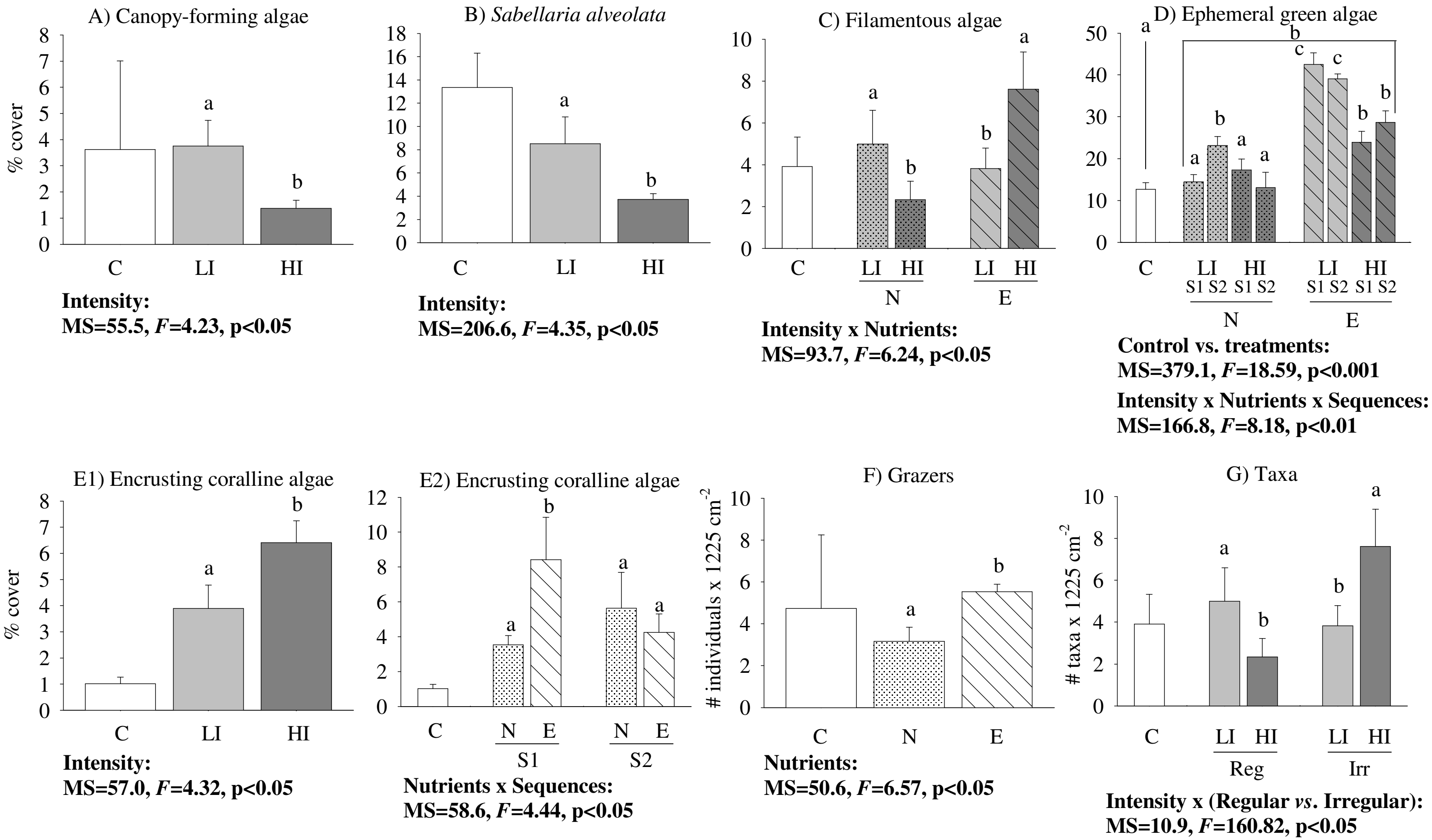

Fig. 4 Bertocci et al.

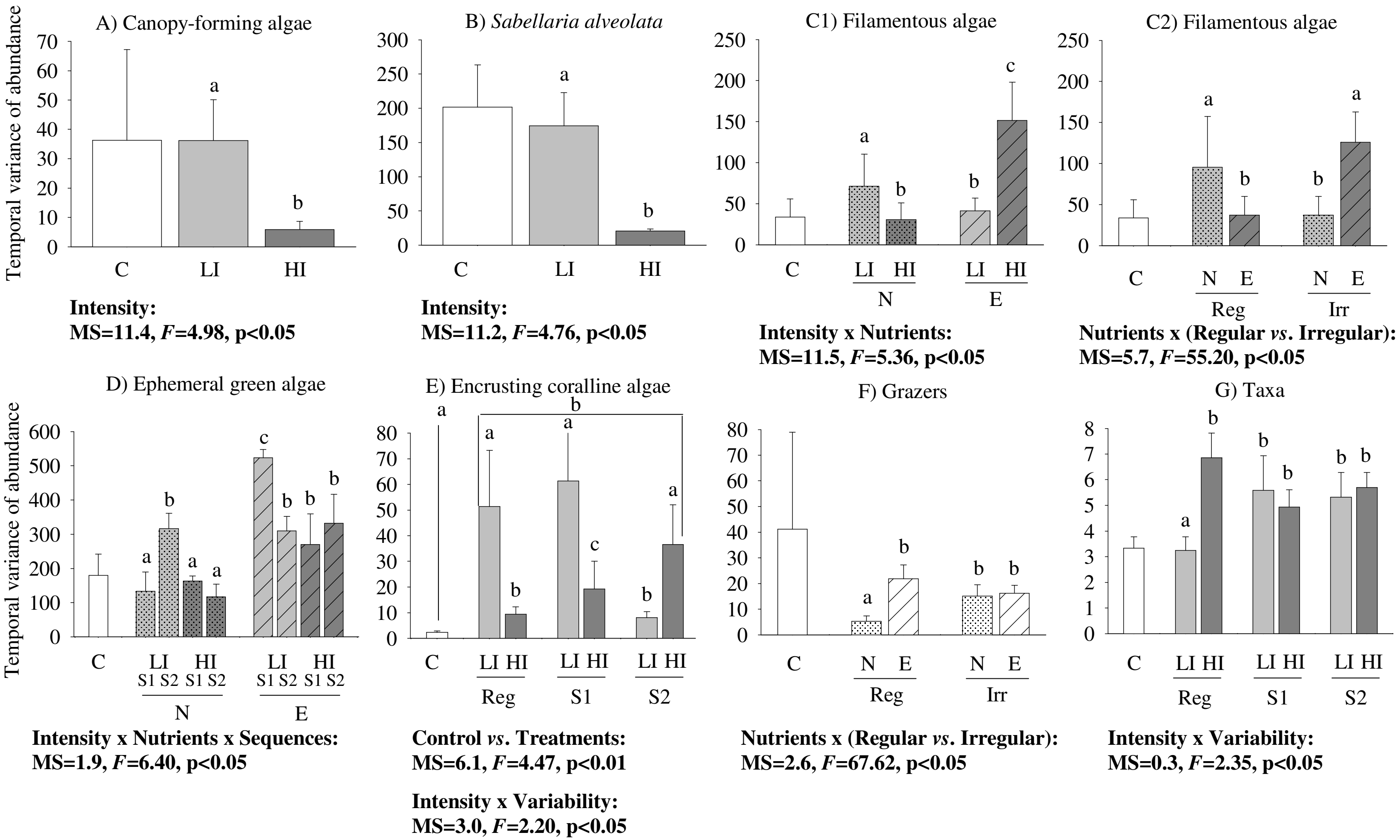

Fig. 5 Bertocci et al.